Changes in heat production by mature cows after changes in feeding level[1,2]

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ABSTRACT: We hypothesized that adaptation of heat production in the realimented cow would occur over an extended period, and the length of time would be influenced by the level of feed. Our objectives were to quantify the changes in heat production of cows after feed restriction and to quantify the effect of level of realimentation on the dynamics of heat production in lightweight cows. Forty 4-yr-old nonpregnant, nonlacting cows (4-breed composite: 1/4 Hereford, 1/4 Angus, 1/4 Red Poll, and 1/4 Pinzgauer) were randomly assigned to receive 1 of 4 levels of a common alfalfa hay source. All cows were feed-restricted [50.0 g of DM/metabolic body size (MBS, kg of BW$^{0.75}$); period 1], and individual fed heat production measurements were taken 0, 7, 13, 28, 56, and 91 d after feed restriction (period 1). In period 2, cows were fed their assigned feed level for their treatment after d 91 of restriction: 50.0 (T50.0), 58.5 (T58.5), 67.0 (T67.0), and 75.5 (T75.5) g of DM/MBS. Measures were taken at 7, 13, 28, 42, 56, 91, 119, and 175 d. In period 3, all cows were fed 75.5 g of DM/MBS after their 175-d measurement, and measures were taken at 7, 14, 28, 56, and 112 d later. In period 1, heat production decreased rapidly during the first 7 d of feed restriction, and heat production continued to decrease during the 91-d restriction. Heat production increased rapidly within the first 7 d, but chronic adaptation continued for T75.5 and T67.0 cows. In period 3, heat production increased rapidly during the first 7 d. Heat production scaled for metabolic body size tended to differ among treatments ($P = 0.11$). Daily heat production increased by 2.5 kcal/d. These data suggest that there is not a lag in heat production during realimentation and that increased recovered energy is associated with a rapid increase in heat production.

Key words: cow, energy, heat production

INTRODUCTION

The cost of feed for the cow herd represents a major production expense associated with beef production. Improving the efficiency with which cows use feed is a potential mechanism for improving production efficiency of beef cattle. Nutrient requirements of the cow change throughout the year as a result of the physiological demands placed on the cow. Stage of pregnancy and stage of lactation both contribute to nutrient requirements. If nutrient intake exceeds nutrient requirements, cows retain energy and conversely when nutrient intake is less than requirements, cows lose body energy. This fluctuation in tissue energy represents the use of nutrients stored as body tissues for other physiological functions. Using the cow's ability to store nutrients in body tissues represents a potential mechanism to improve the economic efficiency of beef production. We reported (Freetly et al., 2000, 2005) that weight cycling can be used in cows to alter the pattern by which feed is offered. In an earlier study, we reported that mature cows that have previously been feed-restricted have a greater efficiency of energy gain when they are refed compared with cows fed at a constant level to maintain BW (Freetly and Nienaber, 1998). However, this increase in efficiency was temporal, decreasing with time. Determining the pattern of change in efficiency of gain will be required in optimizing a management system that utilizes weight cycling. Understanding the pattern of change in efficiency of gain is also important in designing studies that require precise estimates of feed efficiency.

Energy metabolism has long been used as an index of nutrient use. We have demonstrated that in both the growing heifer and mature cow, metabolic rate increases and then decreases with change in nutrient availability (Freetly et al., 2003). In the heifer, the time required to reach a new steady state when nutrients are increased is in excess of 5 wk (Freetly et al., 2003). We hypothesized that adaptation of heat production in the realimented

cow would occur over an extended period of time and the length of time would be influenced by the level of feed. Our objectives were to quantify the changes in heat production of cows after feed restriction and to quantify the effect of level of realimentation on the dynamics of heat production in lightweight cows.

MATERIALS AND METHODS

All animal procedures were reviewed and approved by the US Meat Animal Research Center Animal Care and Use Committee.

Forty nonpregnant, nonlacting cows (4-breed composite: 1/4 Hereford, 1/4 Angus, 1/4 Red Poll, and 1/4 Pinzgauer), which were trained to be used with indirect calorimetry, were used in the study. Cows were trained to eat in and become comfortable with the calorimetry equipment. At the time of the first calorimetry measurement, cows were 4 yr of age.

Ten cows were randomly assigned to each of 4 nutrient treatments. Fifteen weeks before the beginning of the study, cows were weighed and cow BW at a BCS of 5.5 was calculated by adding 45 kg for every BCS less than 5.5 or subtracting 45 kg for every BCS score over 5.5 (NRC, 1996). All subsequent feed allocations were based on this BW. Cows were offered 67.5 g of DM/metabolic body size (**MBS**, kg of $BW^{0.75}$) of chopped alfalfa hay (10.2 cm screen) daily for 15 wk before feed restriction began. The hay was cut in full bloom and sun-cured and had an estimated ME of 1.85 Mcal/kg. Five cows were kept in each pen (493 m^2) and fed individually by use of Calan electronic headgates (American Calan Inc., Northwood, NH).

Twenty-four hours before calorimetry measurements were taken, cows were moved to individual stalls in a barn. On the morning of the calorimetry measurement, each cow's head was placed in a portable respiration box. The daily meal was provided and the box was closed. Flow through the box was allowed to stabilize before O_2, CO_2, and CH_4 exchanges were determined for the next 23 h. Cow BW were taken at the beginning and end of the 23-h calorimetry measurements, and reported BW was the average of the 2 measurements.

The portable respiration box was 0.76 × 0.76 × 1.78 m and was constructed with an aluminum frame and covered with 5-mm-thick clear acrylic sheets. The box had a 28 × 117 cm opening fitted with a vinyl hood, which was attached around the animal's neck to provide a seal between the box and animal. The bottom of the box was constructed with a hopper for feeding and boxes were plumbed with a water bowl. Oxygen, carbon dioxide, and methane exchange were determined by pulling air through the box across a temperature-compensated, dry test meter to determine airflow exiting the box. Real-time air temperature and humidity were determined with a Pace Temperature/Relative Humidity Sensor (TRH-100) attached to a Pace Data Logger (XR440, Pace Scientific, Mooresville, NC). Proportional samples of air entering the box and exiting the box were collected into
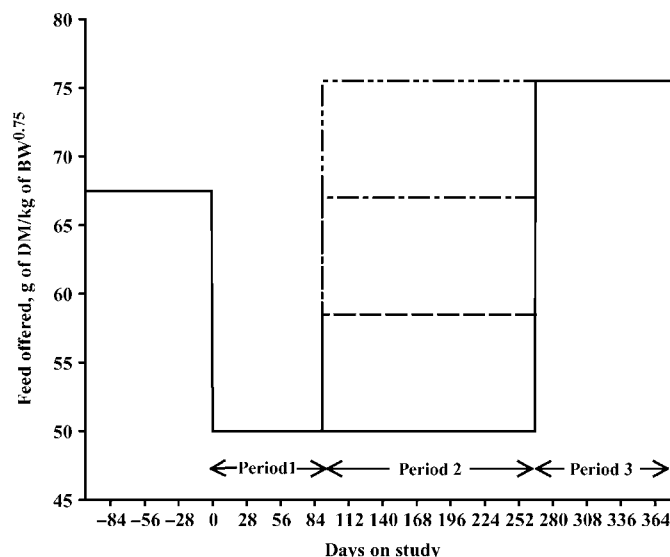

Figure 1. Dry matter offered to cows on study. Before feed restriction, cows received 67.5 g of DM per metabolic body size (MBS, kg of $BW^{0.75}$) per d. The feed restriction lasted 91 d, and all cows were restricted to 50 g of DM per MBS per d (period 1). Period 2 lasted 175 d, and cows received 50.0 g of DM per MBS per d (—, T50.0), 58.5 g of DM per MBS per d (— —, T58.5), 67.0 g of DM per MBS per d (— · —, T67.0), or 75.5 g of DM per MBS per d (— · · —, T75.5). Period 3 lasted 112 d, and all cows received 75.5 g of DM per MBS per d.

gas bags to give a composite air sample for the collection period for each box. Gas bags (PCM, Oak Park, IL) were constructed of a polyethylene/aluminum/Mylar laminate. System recovery of O_2 and CO_2 were routinely determined by using combustion of ethanol within the box. During recovery measurements, a bucket was placed in the vinyl hood where an animal's neck would normally be. Recovery of O_2 and CO_2 ranged from 98.5 to 101.5%.

Air samples were analyzed for O_2, CO_2, and CH_4 as described by Nienaber and Maddy (1985). Twenty-three-hour measurements were converted to daily measurements by multiplying by 1.043478. Heat production was calculated using the O_2 exchange and the respiratory quotient (Kleiber, 1975). Recovered energy (**RE**) was calculated as the difference between ME intake and heat production.

The entire study lasted 378 d and was divided into 3 sampling periods. The study began in the month of June. Ambient temperatures during calorimetry were 15.6°C for winter months, and temperatures were seasonal during the summer months. Sample period 1 consisted of all cows being feed-restricted at a common feed intake for 91 d. In sample period 2 (d 92 to 266), 1 group of cows remained on the restricted level of feed and 3 other groups (10 cows each) were fed a greater amount of feed. In sample period 3 (d 267 to 378), all cows received the greatest level of feed in sample period 2 (Figure 1).

During the feed restriction (period 1), all treatment groups received 50.0 g of DM/MBS after the initial calorimetry measurement. Subsequent individual calorimetry measurements were taken 7, 13, 28, 56, and 91 d after feed restriction.

During period 2, cows were fed their assigned feed level for their treatment after the last measurement in period 1: treatment **T50.0** continued to receive 50.0 g of DM/MBS, treatment **T58.5** received 58.5 g of DM/MBS, treatment **T67.0** received 67.0 g of DM/MBS, and treatment **T75.5** received 75.5 g of DM/MBS. Subsequent measures were taken at 7, 13, 28, 42, 56, 91, 119, and 175 d after the new feed levels were offered (Figure 1).

During period 3, all cows were fed 75.5 g of DM/MBS after the last measurement in period 2. Subsequent measures were taken at 7, 14, 28, 56, and 112 d after the new feed level was offered.

Heat production (unscaled and scaled for MBS) and RE (d 0 through 91) during the initial feed restriction (period 1) were fit to the nonlinear function described by Equation 1:

$$f(t) = [(A \times t) + B] + [C \times e^{(k \times t)}]. \qquad [1]$$

Body weight was fit to similar nonlinear function: $f(t) = A + [C \times e^{(k \times t)}]$. Variable t is the time in days after a change in feed level. Parameter estimates for A, B, C, and k were determined by calculating the least sums of squares for the model using the Gauss-Newton procedure. The analyses were conducted with the SAS (v. 8.00, SAS Inst. Inc., Cary, NC). Residual biases were tested by regressing model residuals on predicted values and testing if the mean residual differed from zero.

Dynamic responses in period 2 for treatments T75.0, T68.5, and T58.5 were initially tested using Equation 1, with the final measurement on d 91 of period 1 as time zero. Model residual biases were tested as described for period 1. Dynamic responses for treatment T50.0 were tested over the same range of data, first using a quadratic equation on time, and if the quadratic term was not significant at $P < 0.05$, then with a linear equation on time. If Equation 1 failed to fit the data for treatments T75.0, T68.5, and T58.5, then quadratic and linear effects of time were tested from d 7 through 175, as described for treatment T50.0.

Dynamic responses in period 3 were initially tested with Equation 1; the final measurement in period 2 was the time zero value for treatments T67.0, T58.5, and T50.0. Dynamic responses for treatment T75.0 were tested over the same range of data, first using a quadratic equation on time, and if the quadratic term was not significant at $P < 0.05$, then with a linear equation on time. If Equation 1 failed to fit the data for treatments T68.5, T58.5, T50.0, then quadratic and linear effects of time were tested from d 7 through 112 of realimentation. If Equation 1 failed to describe the data, differences among treatments were analyzed using a step-down approach. The response variable of scaled heat production was fit with a split-plot model that included animal nested in treatment, treatment, $time^2$, time, treatment $\times time^2$, and treatment $\times$ time. Time was tested as a continuous variable. Treatment effects were tested with the animal nested within treatment as the source of error. Terms that were not significant at the 0.05 level were removed from the model in a step-wise manner beginning with the greatest ordered variables.

Differences in efficiency of energy retention scaled for metabolic body size between days after realimentation in period 2 were tested with analyses of covariance. The model included days realimented as a fixed effect and metabolizable energy intake scaled for metabolic body size as a continuous effect, and their interaction.

Due to equipment failure, 1 observation was not taken at 28 d and 91 d of feed restriction; 1 observation in the T67.0 at d 7 and 1 observation each from T50.0, T58.5, and T67.0 at d 175 were not taken during realimentation period 2; and 1 observation each from T50.0, T58.5, T67.0 at d 7 and 1 observation from T67.0 at d 14 were not taken during realimentation period 3.

RESULTS

Period 1—Restricted Feeding

Feed restriction resulted in DMI decreasing from 7.74 ± 0.07 to 5.70 ± 0.06 kg/d. Residual analyses suggest that the logistic function presented as Equation 1 described the decrease in heat production. The slope of residuals regressed on predicted heat production did not differ from zero (−0.000006 ± 0.09; $P = 1.0$), and the mean residual did not differ from zero (0.04 ± 82; $P = 1.0$). Like with heat production, Equation 1 described the decrease in scaled heat production. The slope of residuals regressed on predicted scaled heat production did not differ from zero (0.00005 ± 0.7; $P = 1.0$), and the mean residual did not differ from zero (0.03 ± 0.5; $P = 0.96$). An exponential decay equation described the decrease in BW. The slope of residuals regressed on predicted BW did not differ from zero (−0.000002 ± 0.2; $P = 1.0$), and the mean residual did not differ from zero (−0.04 ± 3.5; $P = 0.99$). Equation 1 tended to describe the increase in RE from d 7 through 91 of feed restriction. Residual analyses suggest that the equation overpredicted RE on d 7, but the equation fit the subsequent days. The slope of residuals regressed on predicted RE was −2.5 ± 0.3 ($P < 0.001$), and the mean residual was −0.4 ± 0.07 ($P < 0.001$).

The reduction in heat production after feed restriction can be divided into an acute response that occurred within the first 7 d and a chronic response (Figure 2). The function fit to the data predicted that heat production was 85% (Figure 2a) of its initial value at d 7 and that heat production scaled for metabolic body size was 87% of its initial value at d 7 (Figure 2b). There was a chronic decrease in both the scaled and unscaled heat production during the 91 d of feed restriction. Cows were in negative energy balance during the feed restriction. Recovered energy decreased rapidly within the first 7 d
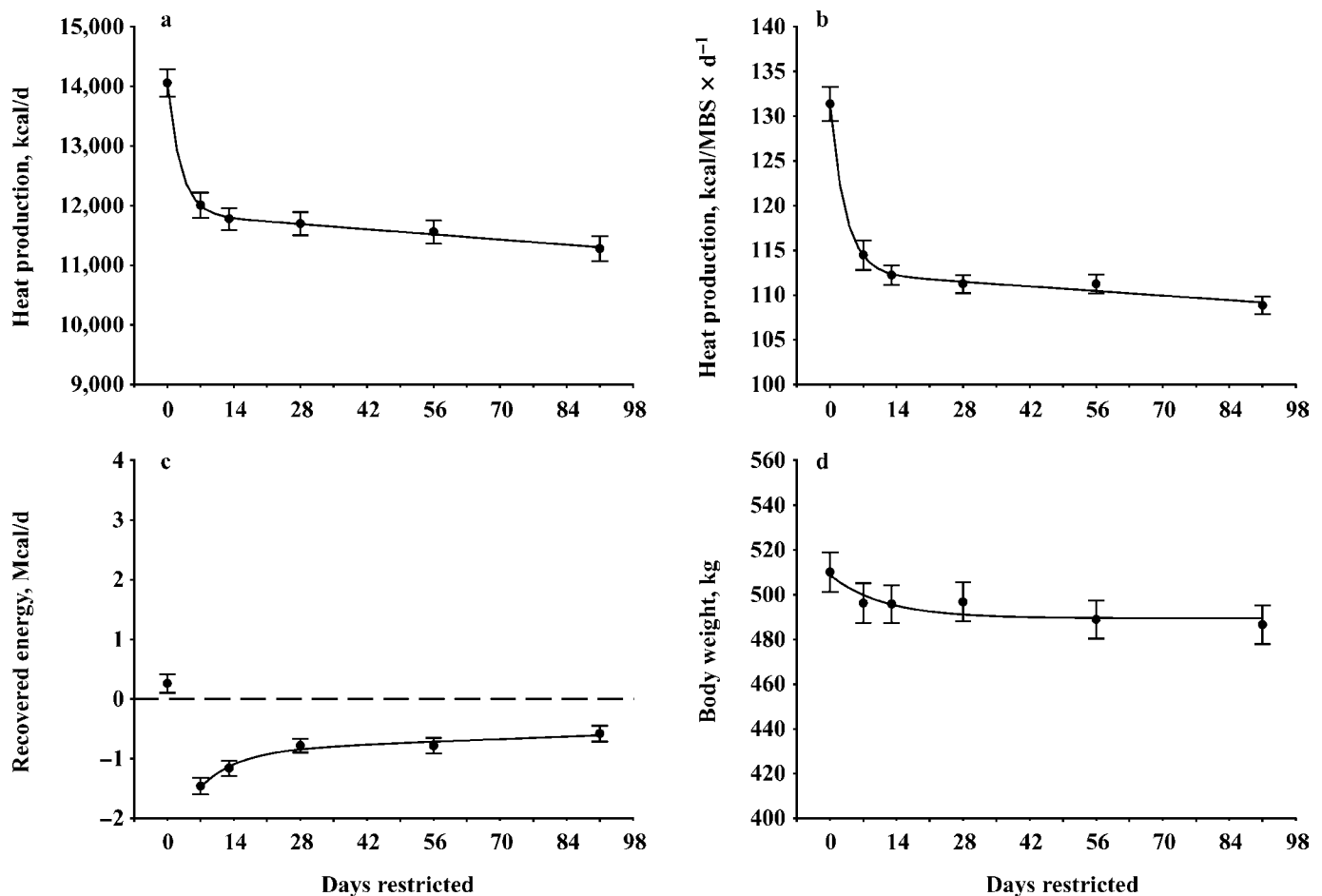
Figure 2. Response of heat production, recovered energy, and BW of mature cows to a decrease in DMI of 67.5 g of DM per metabolic body size (MBS, kg of $BW^{0.75}$) per d on d 0 to 50 g of DM per MBS per d. Data are means and SEM of 40 cows, except on d 28 and 91 (n = 39). Heat production (a) $f(t) = (-6.2 \pm 3.8t - 11{,}863.0 \pm 220.0) + 2{,}193.7 \pm 298.1e^{(-0.3576 \pm 0.2290t)}$. Scaled heat production (b) $f(t) = (-0.037 \pm 0.026t - 112.5 \pm 1.5) + 18.8 \pm 2.0e^{(-0.3103 \pm 0.1277t)}$. Recovered energy d 7 through 91 (c) $f(t) = (0.003 \pm 0.004t - 0.89 \pm 0.30) - 1.46 \pm 1.03e^{(-0.1264 \pm 0.1257t)}$. Body weight (d) $f(t) = 489.5 \pm 6.0 + 19.2 \pm 9.9e^{(-0.0882 \pm 0.1066t)}$.

of feed restriction, but the severity of the negative energy balance was reduced from d 7 to 28 (Figure 2c). Over the course of the feed restriction, cows lost BW.

Period 2—Realimentation to Different Levels of Feed

Equation 1 described the response of heat production to realimentation for T75.5 and T67.0 cows but not for T58.5 and T50.0 cows (Figure 3a). The slope of residuals regressed on predicted values for T75.5 cows did not differ from zero (−0.00002 ± 0.2; P = 1.0), and the mean residual did not differ from zero (0.004 ± 137; P = 1.0). The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (−0.00002 ± 0.2; P = 1.0) and the mean residual did not differ from zero (−0.04 ± 851; P = 1.0). There was not a unique parameter estimate for k for the T58.5 cows. Heat production from d 7 through 175 of realimentation did not differ across time quadratically (P = 0.90) or linearly (P = 0.89) in T58.5 cows. Heat production for T58.5 cows averaged

12,093 ± 150 kcal/d. Heat production in the cows that were not realimented (T50.0) did not differ across time (0 through 175 d) quadratically (P = 0.71), or linearly (P = 0.19), and their mean heat production was 10,601 ± 118 kcal/d.

Heat production scaled to metabolic body size was not described by Equation 1 for T75.5, T58.5, and T50.0 cows (Figure 3b). There was not a unique parameter estimate for k for the T75.5 cows. Heat production from d 7 through 175 in the T75.5 cows decreased over time (−0.037 ± 0.01 kcal/MBS·d⁻¹; P = 0.01). Equation 1 fit the response of T67.0 cows. The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (−0.00001 ± 0.1; P = 1.0), and the mean residual did not differ from zero (0.04 ± 0.5; P = 0.93). There was not a unique parameter estimate for k for the T58.5 cows. Heat production from d 7 through 175 of realimentation changed quadratically (P = 0.04) with the nadir occurring 93 d after realimentation. Scaled heat production in the cows that were not realimented (T50.0) did not differ across time (0 through 175 d) quadratically (P = 0.37),
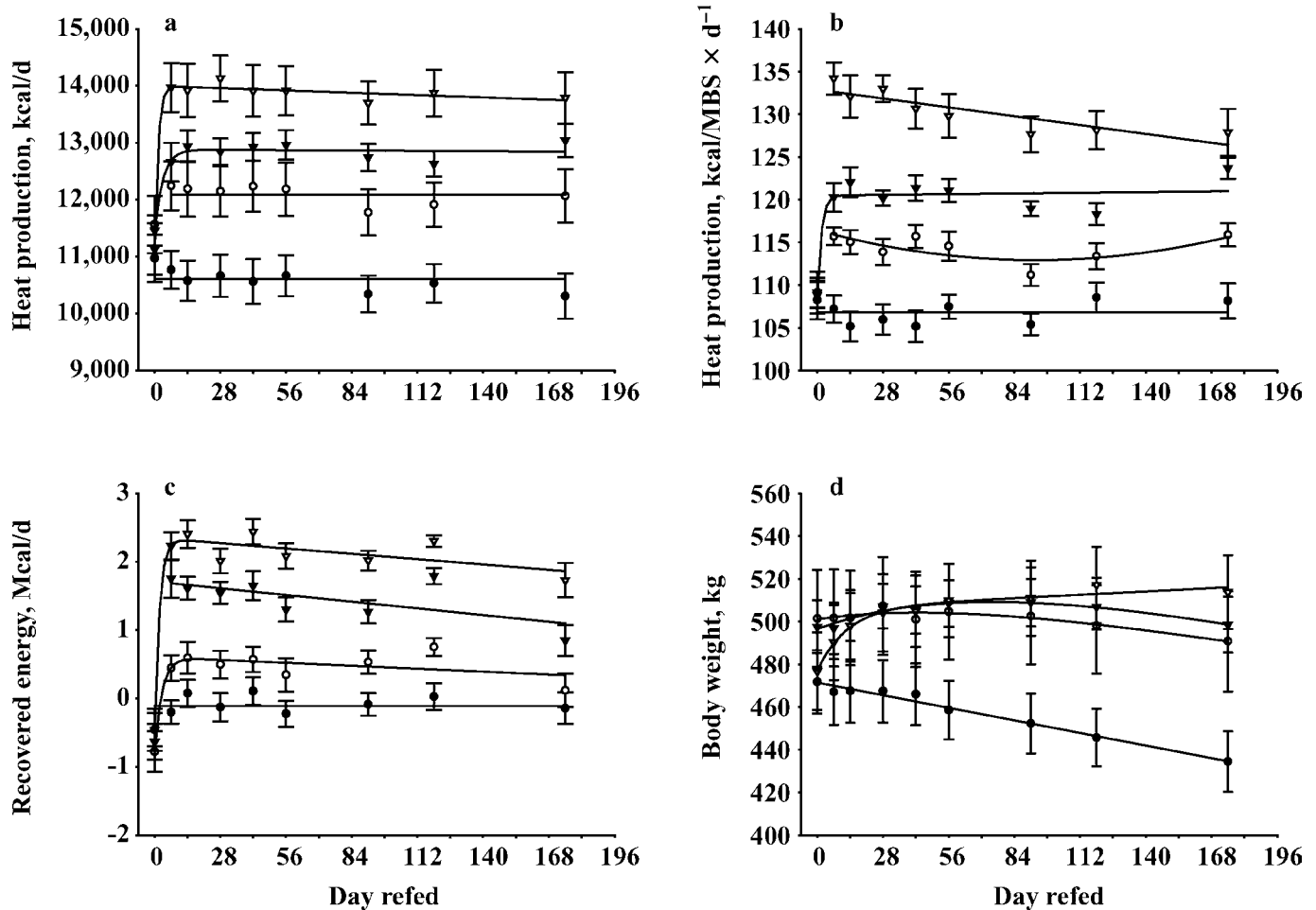
Figure 3. Response of heat production, recovered energy, and BW of mature cows to an increase in DMI of 50.0 g of DM per metabolic body size (MBS, kg of $BW^{0.75}$) per d on d 0 to 50.0 g of DM per MBS per d ($\bullet$, T50.0), 58.5 g of DM per MBS per d ($\bigcirc$, T58.5), 67.0 g of DM per MBS per d ($\blacktriangledown$, T67.0), or 75.5 g of DM per MBS per d ($\triangledown$, T75.5). Data are means and SE of 10 cows, except on d 7 for T67.0 and d 175 for T50.0, T58.5, and T67.0 (n = 9). Heat production (a) T50.0 d 0 through 175 = 10,601 ± 118, T58.5 d 7 through 175 = 12,093 ± 150, and T67.0 d 0 through 175 f(t) = (−0.22 ± 1.98t − 12,882.5 ± 185.2) − 1,426.5 ± 324.1$e^{(−0.2825 ± 0.2300t)}$. T75.5 d 0 through 175 f(t) = (−1.5 ± 3.0t − 13,999.2 ± 276.7) − 2,866.7 ± 502.4$e^{(−0.6878 ± 3.0355t)}$. Scaled heat production (b) T50.0 d 0 through 175 = 106.8 ± 0.6, T58.5 d 7 through 175 f(t) = 0.0004024 ± 0.0001887t^2 − 0.7488 ± 0.0341t + 116.4 ± 1.1, r^2 = 0.06, T67.0 d 0 through 175 f(t) = (0.0027 ± 0.0103t − 120.5 ± 0.9) − 11.7 ± 1.7$e^{(−0.5583 ± 1.0423t)}$, and T75.5 d 7 through 175 f(t) = −0.037 ± 0.014t − 132.9 ± 1.2, r^2 = 0.08. Recovered energy (c) T50.0 d 0 through 175 = −0.11 ± 0.06, T58.5 d 0 through 175 f(t) = (−0.0015 ± 0.0016t − 0.61 ± 0.15) − 1.39 ± 0.26$e^{(−0.3201 ± 0.2480t)}$, T67.0 d 0 through 175 f(t) = −0.0035 ± 0.0013t − 1.70 ± 0.11, r^2 = 0.09, and T75.5 d 0 through 175 f(t) = (−0.0028 ± 0.0015t − 2.35 ± 0.14) − 2.81 ± 0.24$e^{(−0.4827 ± 0.3596t)}$. Body weight (d) T50.0 d 0 through 175 = −0.21 ± 0.09 + 471 ± 7, r^2 = 0.07, T58.5 d 0 through 175 f(t) = (−0.18 ± 1.60t − 523.5 ± 349.6) − 22.5 ± 342.4$e^{(−0.0154 ± 0.2239t)}$, T67.0 d 0 through 175 f(t) = (−0.23 ± 0.98t − 542.8 ± 229.8) − 46.3 ± 225.9$e^{(−0.0138 ± 0.0602t)}$, and T75.5 d 0 through 175 f(t) = (0.06 ± 0.18t − 506.3 ± 20.6) − 29.3 ± 24.3$e^{(−0.0786 ± 0.1471t)}$.

or linearly (P = 0.44), and their mean heat production was 106.8 ± 0.6 kcal/MBS·d^{-1}.

Equation 1 described the response in RE for the T75.5 and T58.5 cows but not the T67.0 cows (Figure 3c). In T75.5 cows the slope of residuals regressed on predicted values from Equation 1 did not differ from zero (−0.00002 ± 0.08; P = 1.0), and the mean residual did not differ from zero (−0.00005 ± 0.07; P = 1.0). In the T67.0 cows there was not a unique parameter estimate for k. Recovered energy did not differ across time quadratically (P =

0.90) but decreased linearly (P = 0.009) in T67.0 cows from d 7 through 175 of realimentation (Figure 3c). Equation 1 described the increase in RE in T58.5 cows. The slope of residuals regressed on predicted values for T58.5 cows did not differ from zero (−0.0002 ± 0.2; P = 1.0), and the mean residual did not differ from zero (−0.0003 ± 0.07; P = 1.0). There was not a quadratic (P = 0.30) or linear (P = 0.55) effect for energy retention in cows that did not get an increase in feed intake (T50.0), and the average RE was −0.11 ± 0.07 Mcal/d.
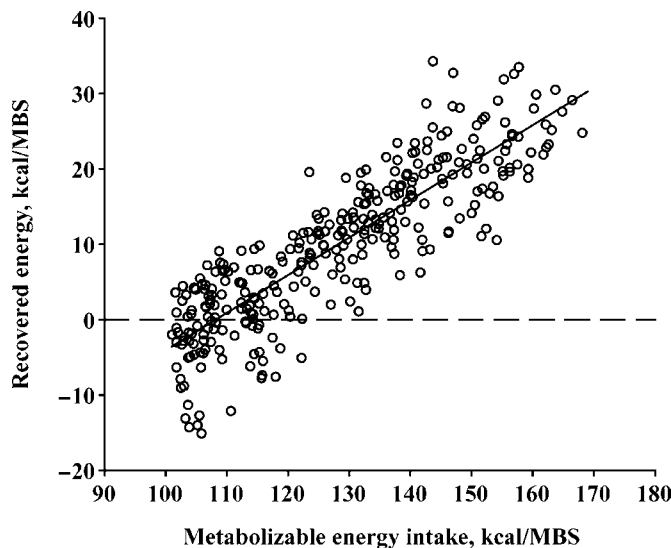
Figure 4. Regression of recovered energy scaled for metabolic body size (MBS, kg of $BW^{0.75}$) on ME intake scaled for MBS for d 7 through 175 of period 2. $f(x) = 0.4976 \pm 0.0161x - 53.8 \pm 2.1$; $r^2 = 0.75$.

Equation 1 described the increase in BW associated with an increase in feed intake for T75.5, T67.0, and T58.5 cows (Figure 3d). The slope of residuals regressed on predicted values for T75.5 cows did not differ from zero (-0.00009 ± 0.5; $P = 1.0$) and the mean residual did not differ from zero (-0.03 ± 6; $P = 1.0$). The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (-0.004 ± 0.8; $P = 1.0$), and the mean residual did not differ from zero (-0.001 ± 4; $P = 1.0$). The slope of residuals regressed on predicted values for T58.5 cows did not differ from zero (-0.0005 ± 0.2; $P = 1.0$) and the mean residual did not differ from zero (0.01 ± 7; $P = 1.0$). There was no quadratic effect of time on BW ($P = 0.93$) for cows that did not get an increase in feed (T50.0), but there was a linear decrease in BW from d 0 through 175 for T50.0 cows (-0.21 ± 0.09 kg/d; $P = 0.015$).

In period 2, the efficiency of metabolizable energy use for RE was 0.498 ± 0.016, and the estimated maintenance was 108 kcal of ME/MBS (Figure 4). Efficiency of energy use did not differ across days after realimentation ($P = 0.99$).

Period 3—Realimentation to a Common Level of Feed

There was no quadratic ($P = 0.36$) or linear ($P = 0.52$) effect of time on heat production in cows that did not get an increase in feed intake during period 3 (T75.5) from 0 through 112 d of realimentation (Figure 5a). The average heat production of T75.5 cows was $13,941 \pm 172$ kcal/d. Equation 1 described the increase in heat production for T67.0 and T58.5 cows (Figure 5a). The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (-0.00002 ± 0.4; $P = 1.0$),

and the mean residual did not differ from zero (0.04 ± 112; $P = 1.0$). The slope of residuals regressed on predicted values for T58.5 cows did not differ from zero (-0.000006 ± 0.3; $P = 1.0$), and the mean residual did not differ from zero (0.02 ± 175; $P = 1.0$). There was not a unique parameter estimate for k for the T50.0 cows. There was not a quadratic ($P = 0.96$) or linear ($P = 0.58$) response of heat production in time for T50.0 cows, and the average heat production from 7 to 112 d after refeeding was $13,146 \pm 179$ kcal/d.

There were no unique parameter estimates for k for scaled heat production in any of the treatments in period 3. From 7 through 112 d of realimentation there was not a linear time effect ($P = 0.11$), but treatments differed ($P < 0.001$; Figure 5b). The average scaled heat production from 7 through 112 d after refeeding was 128.2 ± 0.5 kcal/MBS·d^{-1} for T78.5 cows, 127.0 ± 0.5 kcal/MBS·d^{-1} for T67.0 cows, 130.4 ± 0.5 kcal/MBS·d^{-1} for T58.5 cows, and 131.6 ± 0.5 kcal/MBS·d^{-1} for T50.0 cows.

There was not a quadratic ($P = 0.80$) or linear ($P = 0.39$) response of RE in time for cows that did not receive an increase in feed (T75.5; Figure 5c). The average RE from d 0 through 112 was 2.14 Mcal/d. Equation 1 described the increase in RE after realimentation for T67.0, T58.5, and T50.0 cows (Figure 5c). The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (-0.00005 ± 0.1; $P = 1.0$), and the mean residual did not differ from zero (-0.00003 ± 0.08; $P = 1.0$). The slope of residuals regressed on predicted values for T58.5 cows did not differ from zero (-0.00007 ± 0.08; $P = 1.0$), and the mean residual did not differ from zero (-0.00007 ± 0.06; $P = 1.0$). The slope of residuals regressed on predicted values for T50.0 cows did not differ from zero (-0.00003 ± 0.07; $P = 1.0$), and the mean residual did not differ from zero (-0.0001 ± 0.08; $P = 1.0$).

There was not a quadratic ($P = 0.50$) or linear ($P = 0.77$) response of BW in time for cows that did not receive an increase in feed (T75.5; Figure 5d). The average BW from 0 through 112 d for T75.5 cows was 520 ± 7 kg. Equation 1 described the increase in BW for T67.0, T58.5, and T50.0 cows (Figure 5d). The slope of residuals regressed on predicted values for T67.0 cows did not differ from zero (0.0002 ± 0.6; $P = 1.0$), and the mean residual did not differ from zero (0.002 ± 4.41; $P = 1.0$). The slope of residuals regressed on predicted values for T58.5 cows did not differ from zero (-0.00006 ± 1.2; $P = 1.0$), and the mean residual did not differ from zero (-0.02 ± 8.4; $P = 1.0$). The slope of residuals regressed on predicted values for T50.0 cows did not differ from zero (-0.0001 ± 0.5; $P = 1.0$), and the mean residual did not differ from zero (0.03 ± 5.5; $P = 1.0$).

DISCUSSION

In many cow-calf production systems, nutrient availability will fluctuate throughout the year. As a consequence of fluctuating nutrient availability, the cow's weight and metabolic rate will fluctuate. Predicting the efficiency with which cows use nutrients requires knowl-
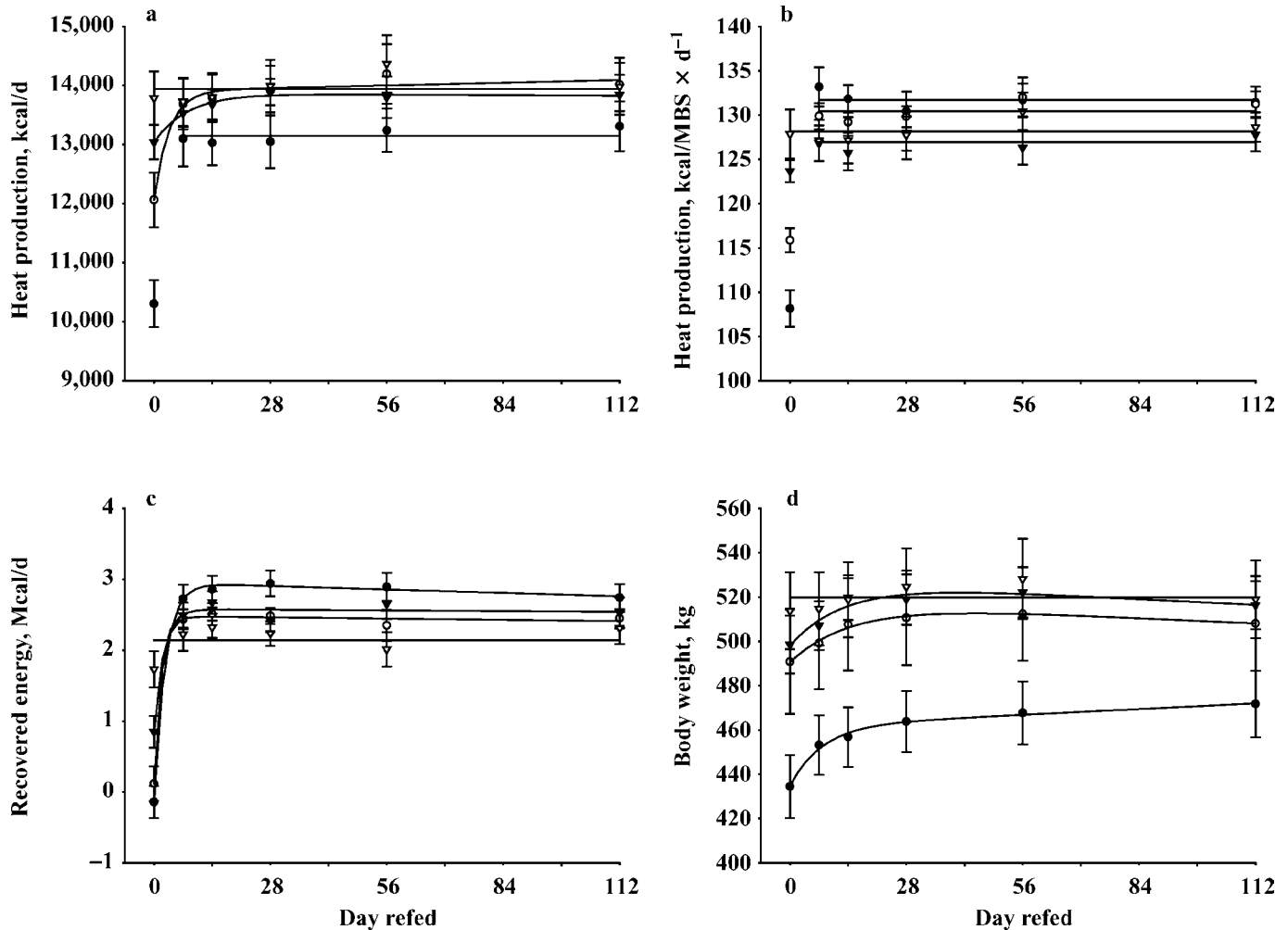
Figure 5. Response of heat production, recovered energy, and BW of mature cows to an increase in DM intake on d 0 of 50.0 g of DM per metabolic body size (MBS, kg of BW$^{0.75}$) per d (●, T50.0), 58.5 g of DM per MBS per d (○, T58.5), 67.0 g of DM per MBS per d (▼, T67.0), or 75.5 g of DM per MBS per d (▽, T75.5) to 75.5 g of DM per MBS per d. Data are means and SE of 10 cows, except on d 7 for T50.0, T58.5, and T67.0 and d 14 for T67.0 (n = 9). Heat production (a) T50.0 d 7 through 112 = 13,146 ± 179, T58.5 d 0 through 112 $f(t)$ = (1.63 ± 6.41t − 13,909.7 ± 443.6) − 1,842.9 ± 634.7e$^{(-0.2752 \pm 0.3161t)}$ and T67.0 d 0 through 112 $f(t)$ = (−0.31 ± 5.26t − 13,864.3 ± 419.4) − 821.8 ± 488.0e$^{(-0.1239 \pm 0.1575t)}$. T75.5 d 0 through 112 $f(t)$ = 13,941 ± 172. Scaled heat production d 7 through 112 (b) T50.0 = 131.6 ± 0.5, T58.5 = 130.4 ± 0.5, T67.0 = 127.0 ± 0.5, T75.5 = 128.2 ± 0.5. Recovered energy (c) d 0 through 112 T50.0 $f(t)$ = (−0.00175 ± 0.00269t − 2.96 ± 0.18) − 3.10 ± 0.27e$^{(-0.3721 \pm 0.1647t)}$, T58.5 $f(t)$ = (−0.00063 ± 0.0021t − 2.48 ± 0.14) − 2.36 ± 0.22e$^{(-0.5801 \pm 0.7146t)}$, T67.0 $f(t)$ =(−0.00034 ± 0.00262t − 2.58 ± 0.17) − 1.73 ± 0.26e$^{(-0.4441 \pm 0.4586t)}$, and T75.5 = 2.14 ± 0.09. Body weight d 0 through 112 (d) T50.0 $f(t)$ = (0.09 ± 025t − 461.7 ± 20.0) − 27.0 ± 23.6e$^{(-0.1301 \pm 0.2502t)}$, T58.5 $f(t)$ = (−0.18 ± 1.60t − 523.5 ± 349.6) − 22.5 ± 342.4e$^{(-0.0154 \pm 0.2239t)}$, T67.0 $f(t)$ = (−0.09 ± 0.28t − 526.9 ± 24.8) − 48.9 ± 25.4e$^{(-0.0783 \pm 0.1306t)}$, and T75.5 = 519.8 ± 6.8.

edge of the time needed to adapt from one feeding level to another. In the current study, heat production was used as an index of metabolic rate. The drop in heat production after a reduction in feed intake can be divided into 3 phases. Phase 1 is the rapid decrease in heat production after feed restriction and is the acute adaptation to feed restriction. Phase 2 is the transitional phase between acute and chronic adaptation. Phase 3 is the period during which chronic adaptation to feed restriction is occurring.

In this study, acute adaptation occurred during the first 7 d of feed restriction. In our previous study (Freetly

and Nienaber, 1998), we found that the acute response occurred before 14 d after feed restriction. Similarly, Ortigues et al. (1993) concluded that acute adaptation occurred within the first 10 d of feed restriction. In the Ortigues et al. (1993) study, half of the acute change seemed to have occurred within the first 4 d of feed restriction. The acute decrease in heat production may be driven partially by the rapid adaptation by visceral and hepatic tissues to restricted feed intake. In growing cattle, oxygen consumption by the portal-drained viscera represents 20 to 28% of the whole animal oxygen consumption, and the liver represents 20 to 30% of the whole
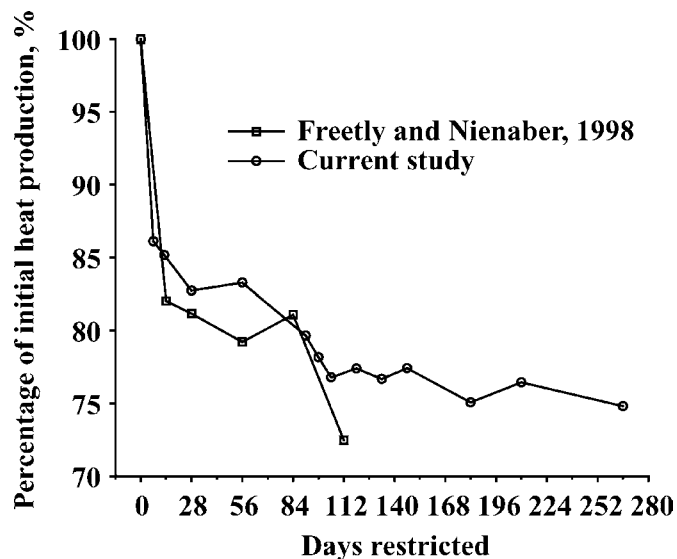
Figure 6. Change in heat production as a percentage of initial heat production in mature cows restricted in DMI in the current study and in a previous study (Freetly and Nienaber, 1998).

Figure 7. Change in heat production as a percentage of initial heat production in mature cows whose feed was increased from 50.0 g of DM per metabolic body size (MBS, kg of $BW^{0.75}$) per d on d 0 to 75.5 g of DM per MBS per d.

animal oxygen consumption (Eisemann and Nienaber, 1990; Reynolds et al., 1991). In steers that are fasted for 3 d, 41 to 66% of the whole body decrease in oxygen consumption can be attributed to the combined reduction in oxygen consumption of portal-drained viscera and liver (splanchnic tissues). In our previous studies in lambs (Freetly et al., 1995), we estimated portal-drained viscera and liver oxygen consumption decreased acutely during the first 14 d after feed restriction. In the same study, we estimated that adaptation to feed restriction would take 29 d for the portal-drained viscera and 21 d for the liver. The time between the rapid decrease in splanchnic oxygen consumption and when these tissues reach a new steady-state corresponds with phase 2 in the current study.

During phase 2, heat production was greater than estimated for the new feeding level. A consequence of this greater heat production was a calculated decrease in RE that remained low until somewhere between 14 and 28 d after feed restriction. The greater heat productions at d 7 and 13 may be associated with the metabolic cost of adapting tissues to the new feeding level. Weight of the gastrointestinal tissues and liver are decreasing, and there may be a metabolic cost associated with catabolizing these tissues.

After 28 d of feed restriction (phase 3), heat production decreased linearly. The decrease in heat production scaled for metabolic body size suggests that the decrease is a function of both a decrease in animal mass as well as a decrease in the metabolic activity of the tissues. In our previous study (Freetly and Nienaber, 1998), we demonstrated that feed-restricted cows eventually return to zero energy balance (maintenance) at a lighter weight. As in the current study, heat production contin-
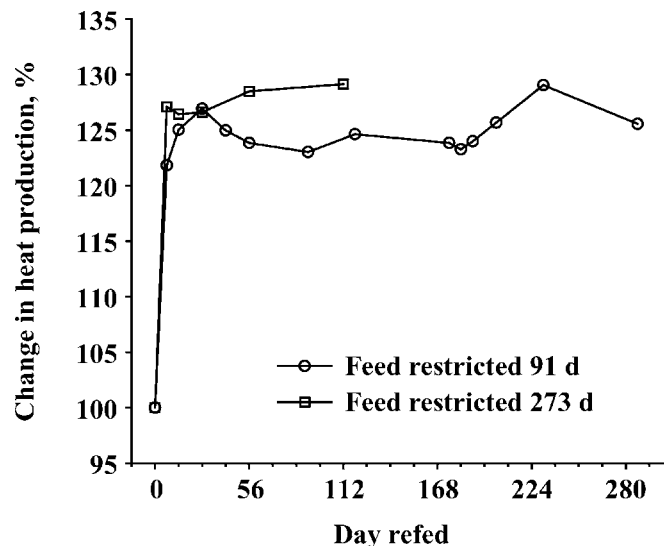
ued to decrease as cows adapted to a lower feed intake. Adaptation in the previous study occurred around 112 d after a 35% feed restriction. In our previous study, heat production decreased rapidly between 84 and 112 d after feed restriction. The current study suggests that heat production decreased through the first 98 d of feed restriction and stabilized during the second period of the experiment. The similar pattern in reduction in heat production (Figure 6) occurred in both studies just before we estimated that the cows were nearing zero energy balance. Previous studies in growing cattle (Trowbridge et al., 1918; Ledger and Sayers, 1977) concluded that to maintain cattle at a given BW, feed had to be continuously restricted. The decrease in heat production observed in phases 1 to 3 was consistent with these earlier findings, suggesting that cattle adapt to prolonged feed restriction. In steers constantly feed-restricted to maintain BW (Ledger and Sayers, 1977), adaptation occurred around 12 wk after feed restriction. In our study, adaptation of the T50.0 cows seemed to occur around 16 wk after feed restriction. The decrease in heat production over time suggests that there is an increase in efficiency of energy use by the animal during feed restriction.

Like feed restriction, acute changes in heat production during realimentation occurred rapidly regardless of the feeding level or previous level of feed restriction (Figure 7). These findings are consistent with our earlier observations (Freetly and Nienaber, 1998) and those of Ortigues et al. (1993). The rapid increase in heat production may partially result from an increase in splanchnic tissue activity. In lambs, the weight of splanchnic tissues increases rapidly after realimentation (Wester et al., 1995) as does oxygen consumption by the tissues.
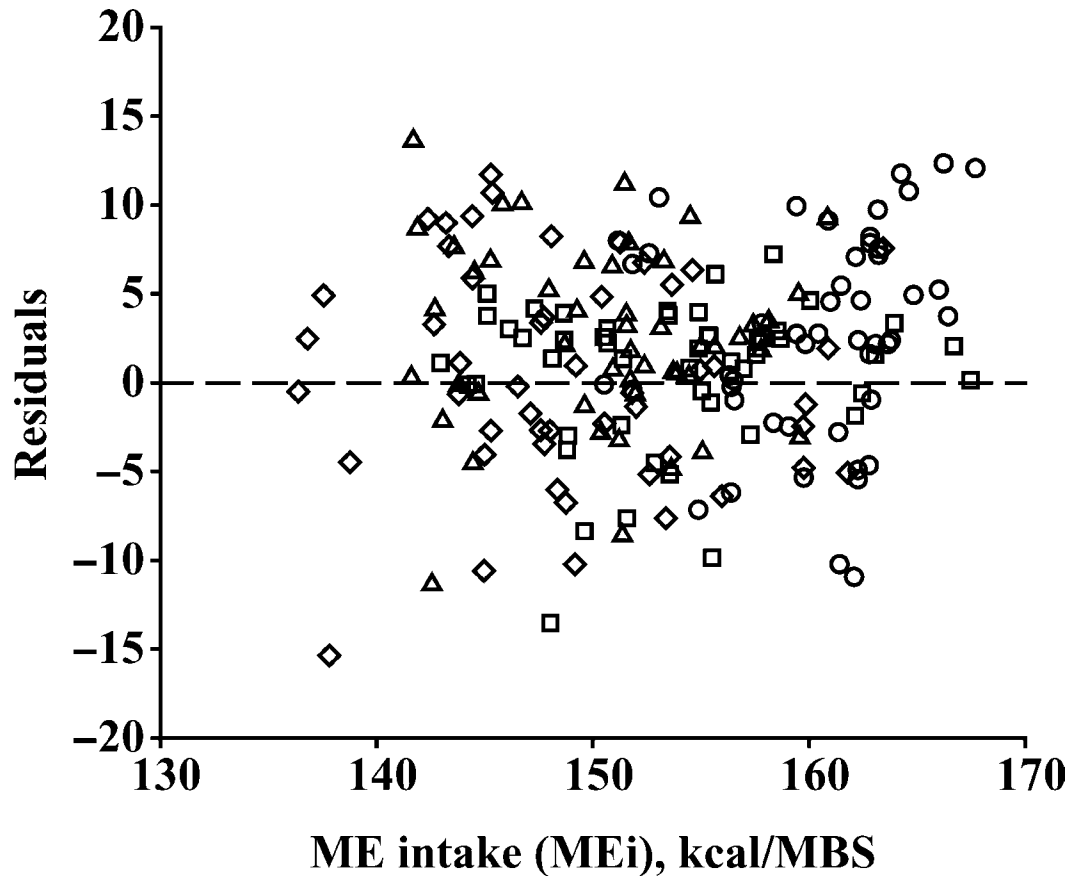
Figure 8. Residuals for recovered energy (RE) in period 3 based on the relationship developed in period 2 (RE = f(MEi) = 0.497 × MEi − 53.8); ○, T50.0; □, T58.5; △, T67.0; and ◇, T75.5. MBS = metabolic body size, kg of BW$^{0.75}$.

Whereas the acute increases in heat production occurs within a similar time frame as the acute phase of feed restriction, the results of the current study are mixed with respect to the relative time required for transition and chronic phases of adaptation. In period 2 when cows were realimented to multiple levels from a common level of feed restriction, heat production scaled for metabolic size seemed to have completed the transitional phase within 14 d of realimentation. In period 3, when cows were realimented to a common level of feed intake, they seem to have completed the adaptation phase within 7 d of realimentation.

Typically in beef production, the mature cow's energy requirements are dynamic, and frequently the cow's nutrient availability is temporal. As a result of these dynamic changes in energy requirements and availability, the cow is frequently losing or gaining tissue energy even though she is not in an active state of growth. The classic definition of energy maintenance is when an animal is in zero energy balance. Estimating maintenance requirements in mature cows can vary with the experimental model used to estimate maintenance requirements. Caution must be applied when interpreting studies that report maintenance requirements for cows. The first question that needs to be addressed is what degree of body fatness is being maintained. Jenkins and

Ferrell (1997) demonstrated that cows fed to weight stasis (presumably maintenance) differed in the degree of body fatness. We have previously demonstrated that feeding cows different fixed levels of feed results in the same cows reaching zero energy balance (maintenance) at different weights. During period 2, we estimated maintenance to be around 108 kcal of ME/MBS, which is in general agreement with that predicted by Moe and Tyrell (1972) for pregnant cows (101 kcal of ME/MBS). However, cows fed 108 kcal of ME/MBS will not maintain a body condition score of 5.5. Estimates of maintenance in lactating cows have been typically greater than those reported in this study (Flatt et al., 1967; Patle and Mudgal, 1977). Incorporated into these greater estimates of maintenance in lactating cows is the increased metabolic activity of tissues such as the liver, digestive tract, and mammary gland that support milk production compared with the nonlactating cow. Estimates of maintenance in this type of experimental model are dependent on the feed level cows were initially stabilized to before realimentation begins.

In period 3, T58.5, T67.0, and T78.5 cows were fed their respective feed levels for 175 d before realimentation, and T50.0 cows were fed 273 d before realimentation. Realimenting cows to a common feed level from different levels of feed restriction was a different experi-

mental model than that in period 2. To compare experimental models, the regression equation developed in period 2 to describe the relationship between RE and metabolic energy intake was used to predict RE in period 3. The model underpredicts residuals for the T50.0 (residual = 2.68 ± 0.84; P = 0.003) and T67.0 (residual = 2.53 ± 0.73; P = 0.001) cows (Figure 8). Residuals did not differ from zero for the T58.5 (residual = 0.59 ± 0.58; P = 0.31) and T75.8 (residual = 0.42 ± 0.86; P = 0.63) cows. These findings suggest that T50.0 and T67.0 cows may have had a greater maintenance, a less efficient use of ME for RE, or both compared with cows in period 2. The greater scaled heat production of T50.0 cows in period 3 is consistent with the high residuals, but the T67.0 cows had a lower scaled heat production, which is not consistent with a lower maintenance or efficiency. These findings suggest that a single predictor of maintenance and efficiency was not adequate to describe energy retention in cows that differ in nutritional history.

In this study, RE was calculated as the difference between ME intake and heat production. Metabolizable energy intake was calculated by multiplying a constant energy density for the feed times the DMI. Errors associated with assuming a constant energy value for the hay are reflected in the RE estimates. In a previous study with brome hay, there was no effect of feed restriction or refeeding on ME density of brome hay, suggesting that a constant value could be used in this study (Freetly and Nienaber, 1998). Incorrectly assigning an energy density to the hay would result in a constant error in the estimates of the RE, but patterns of RE over time should remain the same.

In summary, acute adaptation of heat production to feed restriction and realimentation occurs within the first 7 d. Chronic adaptation to changes in nutrient levels occurs over extended periods. Experiments that use switchback or Latin square designs need to account for the long periods of adaptation. These data suggest that there is not a lag in heat production during realimentation and that increased energy retention is associated with increased heat production.

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